ON CERTAIN FEATURES OF THE DEVELOPMENT OF THE SALMON.

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So much has been written upon the anatomy and development of this fish by eminent authorities that I approach the subject with a certain hesitancy. The development of the skull has been elaborately worked out by W. Kitchen Parker. The skeleton of the adult has been figured in great detail by Bruch in a magnificent monograph, while the general development has been repeatedly discussed by investigators during the last century with more or less thoroughness. Notwithstanding this, it may be truly said that our knowledge of the exact details of some features of its development is still imperfect, even though such able embryologists as Œllacher, Balfour, His, Hoffmann, and Ziegler have devoted considerable attention to it and its allies within a period extending over scarcely more than the past decade.

The early stages of development have been investigated by Œllacher, His, and Ziegler, with such opportunities that can only be enjoyed by one who is near a locality where the spawning or oviposition of the adults is in progress. I can therefore add nothing to the information given us by those writers, but all that will concern us at present is the arrangement of the blood-vascular system at the time of hatching, some of the impairments which this system suffers when the young fishes are under the care of the fish-culturist, and the development of the fins.

The material used in this investigation consisted of recently-hatched embryos of the land-locked salmon, *Salmo salar*, var. *sebago*. I have carefully drawn a live specimen several times enlarged by the help of the camera lucida, as represented in Fig. 1, in order especially to show the arrangement of the vessels on the vitellus, the distribution of the rose-colored oil drops in the latter, and the vessels and venous sinus in the tail.

The mode of development and outgrowth of the fins is especially interesting, the more so since Professor Cope has recently reached the conclusion that many of the so-called "Ganoids" of the Palæozoic rocks seem really to be affiliated to a great and important order of existing fishes embraced by that author under the term *Isospondyli*, which includes the existing Salmonoids, Clupeoids, Hyodonts, Albulids, &c. As it therefore seems that the salmon belongs to a very ancient series of forms dating back phyletically to the Devonian, it may be well for us to examine into the development of the fins to see if that process would really give countenance to Professor Cope's views.

I. *The vertical fins.*—This set of fins is developed from a median fold extending from a vertical slightly behind the pectorals back over the end of the tail, thence forward on the ventral side to the posterior side

of the yelk-sac, the ventral part of the fold being interrupted only by the posterior part of the gut at *v*. Fig. 1. This fold at the time of hatching contains simple embryonic rays throughout its entire extent, these being indicated in Fig. 1 by the fine linear striation apparent for the whole length of the fold in the engraving. These embryonic rays, as they have been called by A. Agassiz, I will call *actinotrichia*, from their slender, unsegmented, hair-like appearance; they are developed from special cells of the mesoblast, which I have named *pterygoblasts* elsewhere. These actinotrichia exceed in number the permanent rays of the adult at least ten-fold. The latter are in fact in great part formed by the fusion of a number of these actinotrichia lying side by side.

The extent to which actinotrichia are developed in the median fin-fold at the time of hatching, however, varies very greatly in different genera. In the recently hatched salmon, which passes through a prolonged period of incubation, these rudiments of the future permanent rays are very numerous, far more so than is the case with most other forms at the time the embryo escapes from the egg. In the Spanish mackerel and in *Gadus* the actinotrichia are not well defined until some time after hatching, and then only in the posterior end of the median tail-fold and in the pectoral fin-fold. As a rule, actinotrichia, (horny-fibers of Balfour), appear first in the anterior paired fins ; this is the case in the salmon, in which these primitive rays are well marked in the pectoral about the time the ventral fin-folds *vt* become well defined.

As urged in my paper " On the origin of heterocercy," the presence of actinotrichia throughout the whole extent of the fin-folds of the embryos of the salmon is an illustration of the Hæckelian principle, viz, that the ontogeny of a form is usually an epitome of the phylogeny of the same. The persistence of the pneumatic duct and the presence of adipose fins are also to be considered in this connection, since both are archaic characters, the first especially.

The permanent dorsal rays of the salmon are formed from the actinotrichia developed in the anterior part of the median fold *d*, *fig.* 1, towards which radial muscles are shoved out at an early stage, as shown by the evenly stippled intervals at the base of this part of the fold. The fold in the interval between the dorsal and soft dorsal atrophies with the further growth of the young fish, the actinotrichia of this interval also disappearing with the fold.

The next portion *sd* of the median vertical fold which is perceptibly widened, gives rise to the soft dorsal or " adipose fin." The actinotrichia of this fin never pass beyond their embryonic condition, so that it is said by the comparative anatomists to contain horny fibers. The whole of the Plectospondyli except the *Characinidæ* have lost their adipose fins, and thus have but one dorsal remaining. The herrings and salmonoids or *Isospondyli* would therefore seem to stand in an ancestral relation to the carps, suckers, and minnows, or *Plectospondyli*. It is at

any rate obvious that the protopterygian condition of the adipose fin is a less specialized and more archaic one than that of its complete atrophy.

The interval between the soft dorsal and the caudal is in part atrophied. The posterior part of this interval, however, gives rise to the short accessory rays of the dorsal edge of the caudal.

The truly dorsal part of the median fin-fold of the embryo salmon ends at the notch n, towards which the urochord, later the urostyle, is directed. At this point the proximal ends of the dorsal and ventral actinotrichia embedded in the fold converge in a penniform manner. The actinotrichia below the notch n and extending out into the caudal lobe cd give rise to the prolonged caudal rays, while those in the ventral part of the fold just in front of the caudal lobe give rise to the inferior accessory caudal rays.

The fold in the interval between the caudal and anal a atrophies, together with its contained actinotrichia, while those in the widened anal part of the fold a as far as the vent v give rise to the permanent rays of the anal, into which the muscles of the fin grow at an early stage or at about the same time that those of the dorsal are developed.

The prëanal part of the fold pa in front of the vent, together with its contained actinotrichia, atrophies entirely during further growth and development.

It is thus shown by the development of the salmon that the most primitive type of distribution of the vertical fins of osseous fishes was a continuous one, because of the development of a continuous series of actinotrichia or primitive rays, and that the forms which now exist and most nearly realize this distribution of the rays of the vertical fins are the Dipnoans, in which the rays are also scarcely more than well-developed actinotrichia, several of which, taken in succession, are homologous with a single ray of an adult Teleost.

The Dipnoans present many other embryonic characters which seem to be partially paralleled by what is transitory in the embryo salmon. When we shall know more of the embryology of *Ceratodus* through the efforts of Mr. Caldwell, who has succeeded in obtaining its ova, further comparisons may be instituted between the ordinary Teleostean embryo and that of the singularly specialized mud-fishes.*

Some of the oldest "Ganoids" had the vertebral axis persistently chordal, unmodified anteriorly, and with an extended series of fins, in these respects paralleling somewhat the condition which is transient in the embryo salmon. These seem to me to be good reasons for accepting Professor Cope's views as to the affiliation of certain of the Palaeozoic fishes with the existing Isospondyli, in the absence, as the latter

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* It is important to examine the fin-folds of the tails of the larvæ of such Amphibians as *Pseudis* and *Dactylethra* to determine whether or not actinotrichia are present. Should these earliest representatives of fin-rays be found in any of the Amphibia the abrupt hiatus now existing between the Dipnoans and the latter would, in a great measure, be bridged.

authority states, of all other characters, except the scales, adequate to separate the two.

II. *Paired fins.*—The paired fins of the salmon develop at wide intervals from each other, that is, the ventral pair is separated from the pectoral by an interval of not less than sixteen muscular segments. In *Lophius* the number of muscular segments opposite the interval between the pectorals and ventrals are reduced to four, according to the figures given by A. Agassiz. In other types this interval between the rudiments of the paired fins of the embryo is still further reduced, as for example in *Trachinus vipera** and in *Motella mustela*† in which, according to Brook, but two muscular segments intervene between the earliest rudiments of the pectoral and pelvic fins, so that in these types it may be said that the paired fins develope from almost continuous rudiments. These and *Lophius* seem to develop the rudiments of the paired fins almost synchronously, which is far from being the case with the larvæ of the Physostomous orders, *Ginglymodi*, *Glaniostomi*, *Nematognathi*, *Plectospondyli*, *Isospondyli*, *Haplomi*, and *Enchelycephali*,‡ in which the ventral pair of fins appears late, often after the pectoral is well developed and in active functional use. In most, if not in all, the larvæ of Physostomous species of Actinopteri, as limited by Cope, the ventral pair of fins is later in appearing than the pectoral; on the other hand in the Percomorph and Pediculate divisions of the Physoclistous Actinopteri it seems that in many species the pectoral and ventral limbs appear almost synchronously, the pectoral usually a little more developed than the ventral pair, and separated serially by only two to four myotomes, while this interval in the Physostomous forms may embrace over sixteen muscular segments.

Finally it may be said that the ventral pair of limbs is almost always undergo shifting or translocation forwards in the Physoclistous groups mentioned. The researches of Mr. Brook, cited above, afford additional evidence of the truth of the principle laid down by me in a preliminary notice§ recently published.

The Physoclistous genera, *Gadus*, *Cybium* (*Scomberomorus*) and *Parephippus* seem to be exceptions to the rule spoken of above, as holding in the development of some forms. How far the rule held in the development of the Palaeozoic fishes with ganoid scales and ventral or abdominal pelvic fins, we, of course, now have no means of knowing. These, with the exception of *Dorypterus* and *Blochius*, seem to have had

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* Preliminary account of the development of the Lesser Weever-fish Trachinus vipera, by George Brook, F. L. S., Journ. Linn. Soc., xviii, pp. 274–291, pls. 4, 1884.

† On some points in the development of Motella mustela, Linn., by George Brook, F. L. S., Journ. Linn. Soc., xviii, pp. 299–307, pls. 3, 1885.

‡ The eels are of course permanently without ventrals; the youngest obtainable larvæ of Anguillidæ and the Leptocephalid stages of marine eels show no traces of ventral limb-folds; these forms are in fact permanently apodal.

§ On the Translocation forwards of the Rudiments of the Pelvic Fins in the Embryos of Physoclist Fishes, Am. Naturalist, 1885, pp. 315–317.

the pelvic fin not displaced forward, but normal in position, as in the majority of existing Physostomous Actinopteri.

The belated development of the pelvic fins of some of the *Isospondyli* and *Haplomi* is quite remarkable; in fact, the pectoral in these forms may have the permanent rays pretty well developed before the ventral fin-fold has done much more than begun to develop. The ventral fin-fold, however, in those forms in which it appears synchronously with the pectoral is at first always the smallest, thus showing the effects of an inherited tendency to retard the development of the pelvic fins.

In the salmon the pectoral is functionally developed with well defined actinotrichia lying beneath the investing epidermis, as shown in Fig. 1, by the time the ventral is appearing as a flat, immobile lobe without developed actinotrichia, behind and above the yelk-bag.

III. *The embryonic blood vascular system.*—In the embryo salmon this attains great importance apparently in consequence of the presence of a voluminous yelk which is absorbed by a system of vitelline vessels. A large median aortic trunk *ao*, Fig. 3, is developed under the notochord *ch*, Fig. 4. It is formed from two convergent suprabranchial arteries anteriorly, which receive their blood from the branchial trunks coming from the gills. The aorta extends backward, giving off "intercostals" and intersegmental branches *s* along either side and terminates under and at the end of the urochord. A recurrent vessel then bends down from it and divides into several loops which converge in the caudal venous sinus *sc*, Fig. 3, incorrectly referred to as a "caudal heart" by some writers, as it exhibits no independent pulsations of its own.

From the caudal sinus the caudal vein or cava arises and passes forward towards the body-cavity, where it divides anteriorly into the paired cardinal veins *cr*, Fig. 3. These pass forward to the venous sinus of the heart formed by the Cuvierian ducts into which they empty their contents. The heart lies behind and below the branchial frame-work, and forces only venous blood through the gills. Its anterior chamber or bulbus aortæ is prolonged forward into a truncus arteriosus, which gives off a pair of vessels to each pair of gills. These vessels, after breaking up into a plexus of capillaries, send the arterialized blood through another set of branchial vessels which join a pair of longitudinal trunks, of which the radices aortæ are prolongations posteriorly and the carotids anteriorly. The venous blood from the head is carried back to the heart by way of a pair of jugular veins or anterior cardinals to the venous sinus. The foregoing describes in outline the systemic circulation proper, exclusive of the great portal system, to which the network covering the yelk-bag also properly belongs.

The portal system of the young salmon with the yelk-bag still attached may be said to comprise no less than three successive sets of capillaries. The first of these arise from the caudal and cardinal veins *cr*, and pass from above downward on either side of the intestine to join and fill with blood a large azygous or median subintestinal vein,

si, Fig. 3. This vessel passes forward under and into the liver *L*, where it again breaks up into a plexus of smaller vessels; these then again blend into larger trunks, as shown at *pv*, in Fig. 4, which emerge from the liver to again break up into the capillary net-work *cc*, Fig. 3, which is still better shown in Fig. 1, on the surface of the yelk-bag. This vitelline net-work then joins the vitelline veins *vv* and *vv'*, which blend into a common trunk before joining the venous end of the heart. It will thus be seen that we have no less than five capillary systems in the young salmon, as shown in Fig. 1, if we reckon those of the portal system together with those belonging to the systemic system of vessels. These in their order are: (1) The branchial, (2) the systemic, (3) the intestinal, (4) the hepatic, and (5) the vitelline capillaries.

What the subsequent history of the third and fourth sets may be I have not made out, but the fifth or vitelline set has only a temporary existence, remaining only as long as there is yelk in the yelk-bag. As the yelk is absorbed this system disappears, when the vitelline veins *vv* and *vv'* become portal veins; that is, they carry all of the blood which passes through the viscera back to the heart.

A study of sections of the yelk-sac of the salmon leads to the following conclusions: A well-marked periblastic stratum of plasma, *p*, Fig. 4, invests the yelk. Beneath the periblast lie the oil-drops *o*, *o*, which are largest at the upper part of the yelk, the greater buoyancy of these larger, superior oil globules tends to keep the young fish buoyed up, and functions much in the same way that an air-bladder would, a structure which, by the way, is not yet functional in the young salmon at this stage of growth. In the earlier stages these larger oil-drops, which lie just under the blastodisk or germinal mass, by their buoyancy constantly keep the germ rotated or turned toward the top of the egg.

External to the periblastic layer of the yelk comes the vascular net-work of capillaries, the walls of which are formed, apparently, by a thin sheet of splanchnic mesoblast *vm*, which invests the yelk but which has grown down over the latter at a later period, possibly, than the thin epidermic or epiblastic investment *ep*, Fig. 4. This vascular net-work is obviously the apparatus by means of which the yelk is absorbed superficially from the external plasmodium or periblast of the yelk, a stratum, which, as is well known, contains scattered free nuclei.

The epidermis or epiblast of the young salmon is remarkable amongst fish embryos for the peculiar goblet-shaped cells which are found distributed over almost the entire surface of the embryo. These are shown in a section of the epidermis in Fig. 5, much enlarged. Their function is apparently to secrete a mucilaginous substance for the purpose of protecting the skin of the embryo.

IV. *Diseases or abnormalities which involve the yelk-sac and vitelline*

circulation of salmon embryos.—A discussion of some of the pathological phenomena observed while salmon embryos are under the care of the fish-culturist seem to me to be in place here.

Shortly after hatching many of the young fish in the hatching troughs sometimes show whitish spots on the yelk-sac.   If examined under the microscope it is plain that these spots consist of coagulated or dead yelk material.   Very often the capillaries in the vicinity of these spots are found to be occluded and filled with clots of blood, as if the vessels had been bruised.   In other cases it is found that the capillaries of the liver are occluded so that that organ, which is visible on the left si le of the embryo through the integument, assumes a whitish, abnormal color. Closer examination reveals the fact that the blood no longer circulates through the liver, and that the tissues of the organ are practically dead, as indicated by the white color which they assume.   These conditions lead to the death of the affected embryos in great numbers.   The causes which seem productive of such abnormalities have not been determined with certainty, but it would seem probable that blows or knocks received by the sac from careless handling or the violent and too rapid flow of water over the young fish, so as to carry them violently against fixed objects in the trough, are probably very hurtful and productive of the changes noted.

Still other abnormal changes in the yelk-sac may be noticed here. The most serious is that characterized by the distension of the epiblastic covering of the sac with fluid so that it is lifted up from contact with the yelk more or less extensively.   Usually, this distension only affects the posterior extremity of the sac, but occasionally specimens are observed in which there is a space all round the yelk between the latter and the epiblastic sac.   Sometimes free-blood corpuscles which have escaped from ruptured vessels are found floating about in the fluid contained in the cavity described.   At other times, an extension of the back part of the yelk proper may be prolonged backward into the outer sac, which may become constricted so as to embrace part of the yelk.   As the anterior part of the yelk is then absorbed, the posterior constricted part is finally left hanging to the abdomen by a sort of pedicle formed by the outer sack.   This finally drops off and the young fish survives. The spot where the stalk breaks off on the under side of the embryo heals up and the young fish seems none the worse for having lost part of its yelk, except that it has probably not grown quite so large or so rapidly as its more fortunate fellows.

The plate illustrating the foregoing article is number XII of the present volume.